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THERMOREGULATORY BEHAVIOR OF AMERICAN MARTEN

Aug. 10, 1987

FINAL REPORT TO THE

U.S.D.A. FOREST SERVICE

ROCKY MOUNTAIN FOREST AND RANGE EXPERIMENT STATION

THERMOREGULATORY BEHAVIOR OF AMERICAN MARTEN

U.S. FOREST SERVICE COOPERATIVE AGREEMENT

NUMBER 28-C6-372

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EXPERIMENT STATION

Endotherms in highly seasonal environments are periodically challenged by thermal stress and food deprivation. In temperate and more polar environments, endotherms may experience body core temperature (T_b) - ambient temperature (T_a) gradients that exceed 80°C during the cold season. Accomodation of animals to these temperature extremes involves the interaction of structural, physiological, and behavioral adaptations to increase an animal's individual fitness.

American marten (Martes americana) appear to represent an unorthodox pattern of adaptation to the severe cold to which they are seasonally exposed. Marten possess extremely limited reserves of body fat ($\bar{X}$ = 2.4% of skinned carcass weight, n = 12; Buskirk 1983) that remain fairly constant over the course of the winter. Further, they have fur that is not exceptionally insulative (Scholander et al. 1950), have relatively high surface area/mass ratios as a result of their elongated mustelid body form (Iversen 1972), are active during the coldest weather (Herman & Fuller 1974) and have not been reported to hoard foods. Although marten capture most of their prey in winter from subnivean spaces (Koehler et al. 1975, Strickland et al. 1982) they cover their large home ranges (Strickland et al. 1982) on the snow surface (Raine 1983), where they are exposed to the coldest winter microenvironment in the boreal forest (Pruitt 1978).

T_b and metabolic rate are important variables in the energy dynamics of any thermally stressed endotherm, particularly those with limited energy reserves. By reducing T_b marten could lower

temperature gradients that drive heat flux and, by reducing energy consumption, marten could increase the lengths of time over which they can maintain net energy debit. Although energy conservation could be accomplished by facultative depression of T_b and metabolic rate during periods of rest, such events have not been described for marten. Worthen and Kilgore (1981) reported a lower critical temperature (T_{lc}) for marten of 29°C, a value that does not appear consistent with the boreal and subarctic distribution of this species. If applicable to marten in the wild, such a T_{lc} would suggest that marten are exposed to above-snow T_as below thermoneutrality for most, if not all of the year. Because of the important implications of Worthen and Kilgore's (1981) value, we felt that measurements of metabolic rate in relation to T_a with winter-acclimated marten should be repeated.

We investigated the thermoregulatory behavior and physiology of free-ranging and captive marten in southeastern Wyoming during the winters of 1985-86 and 1986-87. We studied T_b dynamics of free-ranging marten to examine how marten modulate energy loss in response to environmental variables. In addition, we repeated Worthen and Kilgore's (1981) measurements with winter-acclimated marten. Studies of metabolic rate also permitted us to make inferences about rates of heat loss from resting marten.

METHODS

Study area

Free-ranging marten were studied in an approximately 108-km^2 study area in the Medicine Bow Mountains (41° 21' N, 106° 12' W) of

southeastern Wyoming (Figure 1). Elevations in the area ranged from 2500-3300 m. Vegetation included two major forest types, one dominated by Engleman spruce (Picea englemanii) and subalpine fir (Abies lasiocarpa), the other by lodgepole pine (Pinus contorta). Detailed descriptions of the study area have been provided by Oosting and Reed (1952) and Billings (1969).

Long-term data provided by four weather stations within the study area (Wyoming Water Research Institute) indicate mean annual precipitation in the area of about 60 cm, two thirds of which falls as snow. Mean midwinter snow depths (at 3012 m elevation) for 1985-86 averaged 1.92 m, for 1986-87 0.95 m. Long-term mean monthly $\underline{T}_a$ s at 2460 m for December, January and February are -4.4°C, -5.6°C and -5.0°C, respectively (Becker & Alyea 1964). High winds (>5.6 m/sec) are frequent at all elevations throughout winter. The area is used intensively for recreation, with about 140 summer cabins and a public ski area. It is presently under intensive timber management, mostly by clear-cutting 2-60 ha patches.

Field studies

Field studies were conducted from December 1985 to February 1986 and from December 1986 to February 1987. Animals were captured in baited live traps using oil of anise as a chemical lure. Captured animals were transported in a holding box to the University of Wyoming. Under general anesthesia (ketamine hydrochloride, 60 mg/kg body weight, IM), each animal was incised for about 20 mm along the ventral midline through the linea alba. A calibrated temperature-sensitive radiotransmitter 43 mm in

length, 18 mm in diameter and weighing about 16 g (model L, Mini-mitter Co., Sunriver, OR) was inserted through the incision into the abdominal cavity and stitched into the abdominal musculature with 00 silk thread tied around the transmitter. Each marten was equipped with a radio collar weighing about 29 g (BT type, AVM Instrument Co., Dublin, CA). When the animals had recovered fully from anesthesia, 3-16 hours after surgery, they were released at the capture site. Each animal was recaptured at the end of the study and the collar removed. All surgical wounds healed well. A lower premolar was extracted from each animal and age was estimated by staining and counting cementum annuli (Grue & Jensen 1979).

Radio tracking of animals with directional antennas was conducted during daylight hours. When found resting, the location of the resting site was marked and a device which recorded $\underline{T}_b$ data was left within 10 m of the resting site. The recording device consisted of a Realistic model TRC 211 citizen's band transistor receiver with crystals matched to the frequencies of the temperature implants, a solid state timing device with built-in controls for setting the duration of the signals recorded and the interval between readings, and an inexpensive cassette tape deck to record the $\underline{T}_b$-dependent rate of clicks. The timing device sampled transmissions from a single implant for 1 minute every 0.5 hours. After resting sites used by study animals had been identified, recording devices were placed within 20 m of vacant resting sites so that $\underline{T}_b$ data were recorded for animals as they arrived and began to rest. Because of the limited transmission range of the temperature implants (ca. 15 m), most data gathered were for

animals at resting sites, although some data were gathered for animals as they approached and departed. Magnetic tapes of transmitter clicks were converted to $\underline{T}_b$ values manually from calibration curves.

Laboratory studies

Six marten (three males, three females) were captured in the study area in February 1986 and 1987 and housed at the Red Buttes Environmental Biology Laboratory for metabolic studies. They were held in steel cages (0.86 m x 0.77 m x 0.69 m) and provided with wooden nesting boxes (.41 m x .25 m x .23 m) with a single 70-mm diameter entrance hole. Air temperature was maintained at 10°C and photo regime at 10L:14D. Commercial dry cat food and water were provided ad lib and supplemented with small mammal prey.

An airtight respirometer with dimensions identical to those of the nesting box was provided to each animal in turn. The animals were given four days to acclimate to the respirometer as their new nesting site. Then a sliding door was closed over the entrance hole and sealed with rapid-drying window caulking. Tubing from a Neptune diaphragm air pump was connected to an incurrent port, providing a continuous air supply which left the chamber via an excurrent port. The respirometer containing the marten was placed into a 70-mm thick cylindrical cooling jacket built with an inside diameter just large enough to accomodate the respirometer. Both ends of the cooling jacket were then sealed with 51 mm-thick styrofoam lids perforated to accomodate air lines and thermocouple leads.

The jacket received a circulating antifreeze-water mixture from a Precision Scientific 30-1 water bath at a flow of 3 l/minute. Air was passed through 15 m of copper tubing coiled within the cooling jacket to equilibrate the air to the ambient jacket temperature before passing through the respirometer. Air flow was maintained at 3.1 l/minute through the respirometer and was continuously monitored on a Matheson Model 8143 mass flow meter and an Esterline Angus model S-22656 Miniservo strip chart recorder. Excurrent air was passed through a drierite column and a portion channeled to an Applied Electrochemistry model S-3A oxygen analyzer. Percent oxygen was recorded on an Esterline Angus model S-22656 Miniservo chart recorder and oxygen consumption calculated according to the formulas of Depocas and Hart (1957). Air temperature within the respirometer was monitored with a thermocouple projecting into the restind box and was continuously monitored on a third miniservo chart recorder.

Because the respirometer chamber served as a resting box, marten were at rest or asleep as $\underline{T}_a$ was decreased at a rate of approximately 0.1 °C/minute during a seven-hour period beginning around 0900. The $\underline{T}_{lc}$ for each animal was identified as that temperature at which oxygen consumption increased above the resting value for thermoregulatory heat production. The slope of the regression line through oxygen consumption values at ambient temperatures below the $\underline{T}_{lc}$ was used to index each animal's thermal conductivity at rest.

RESULTS

Dynamics of T_b, patterns of resting site use and activity patterns of eight free-ranging marten (six males, two females) were studied during the two winter field seasons. The eight marten were found at resting sites on 127 occasions. A total of 1368 measurements of T_b were made for 93 resting episodes, 69 for animals leaving resting sites and 24 for entire resting periods. The distribution of sampling intensity was not uniform among study animals because animals that used the fewest resting sites contributed most heavily to complete T_b data runs. The highest observed T_b s for individual marten ranged from 37.8 to 41.8°C (Table 1).

Body temperatures of marten generally declined, fluctuated and then increased to an active level during a single resting episode (Figures 2, 3). Depression of T_b during resting episodes averaged 2.9°C and differed among the six animals for which these data were gathered (ANOVA, $F = 25.7$, $P < 0.001$, $n = 87$). The most profound depression of T_b observed during a single resting episode (for marten number 5) was 5.1°C. For animals that depressed body temperature while resting, greatest depression of T_b occurred 1.6-4.0 hours after initiation of a resting episode. The T_b of a juvenile female that weighed 678 g usually rose immediately after entering a resting site (Figure 2c). Minimum T_b s reached during resting episodes ranged from 35.6 to 38.0°C and differed among animals (ANOVA, $F = 27.9$, $P < 0.001$, $n = 87$).(Table 1). In examining the effects of environmental variables on T_b, we

therefore excluded animals (numbers 2 and 8) whose minimum resting T_b s differed markedly from the others. Minimum resting T_b s for these remaining 4 animals did not differ at the $P = 0.05$ significance level. Minimum T_b during individual resting episodes was positively correlated with mean T_a during the resting episode ($r = 0.46$, $P = 0.05$, $n = 19$) and the $\log_{10}$ of duration of the resting episode was negatively correlated with minimum T_b while in the resting site ($r = -0.42$, $P = 0.08$, $n = 19$).

Mean duration of complete resting episodes was 10.0 hours (range = 1.5 - 41.0 hours). The longest observed resting episode (incomplete) lasted 55.0 hours. Duration of resting episodes did not vary significantly among the four animals for which we had data for complete resting episodes, therefore all four animals were included in tests of relationships between the duration of resting episodes and environmental variables. Mean wind speed during the activity period immediately preceeding the resting episode was correlated with the duration of the resting episode ($r = 0.38$, $P = 0.08$, $n = 22$). An interaction variable, "chill," (the product of mean wind speed and mean T_a) was used to index the cooling power of the air during activity periods. "Chill" was correlated with the duration of the resting episode following the activity period for which it was measured ($r = -0.64$, $P = 0.001$, $n = 22$). Although "chill" for the time of resting was also correlated with resting episode duration ($P = 0.01$), we believe that this relationship was an artifact of the autocorrelation of weather conditions before and during resting episodes. Mean duration of 22 activity bouts of known duration was 4.6 hours (SE = 0.73). Although adults and

juveniles were often active during daylight hours, juveniles were active more often during the day than were adults (ANOVA, $\underline{F} = 4.5$, $\underline{P} = 0.08$, $\underline{n} = 8$).

Mean resting metabolic rate (RMR) of six marten was 0.508 ml O_2/g x hour. The measured $\underline{T}_{lc}$ was 16°C (Figure 4), and the conductance was 0.0527 ml O_2/g x hour x°C (Figure 4).

DISCUSSION

The resting metabolic rate of an animal serves as an important indicator of its energy requirements as well as providing a means of intraspecific comparison (Farrell & Wood 1968). For example, the rate of metabolism in mammals is influenced by body size, climate and food habits, all of which are associated with thermoregulation. Small mustelids are unique in their thermoregulatory capacity; they have relatively short fur (Casey & Casey 1979, Chappel 1980) and a high surface area/volume ratio, the latter of which has been cited as an explanation for a generally high metabolic rate and thermal conductance for this group. However, as Iverson (1972) and Knudsen (1979) have pointed out, there are exceptions to this pattern. In our study, the calculated RMR of 0.508 ml O_2/g x hour was close to the predicted value of 0.63 ml O_2/g x hour for mammals of this body mass (RMR = $3.417\ M^{-0.25}$, Kleiber 1961), but lower than the value predicted by Iverson's (1972) equation for mustelids with body masses greater than 1 kg. Similarly, Worthen and Kilgore's (1981) published value of 0.661 ml O_2/g x hour for marten was also below that predicted for a small mustelid based upon Iverson's (1972) equation. Indeed,

as pointed out by Farrell and Wood (1968), many small mustelids may have RMRs close to those of other mammals of similar size if care is taken in determining true resting metabolism. In our study, marten were habituated for several days to a respirometer identical to their nesting box. As a result, these animals were extremely quiescent during the period when $\underline{T}_a$ was depressed. We feel that the lower RMRs reported in this study represent a state of sleep or calmness associated with a very familiar environment. Therefore, the generalization that thermoregulation by small mustelids in cold climates is partially achieved through increased RMR (Scholander et al. 1950) may have significant exceptions. This strategy would be energetically expensive for the marten because of other limitations such as low fat reserves and concomitant metabolic demands associated with their rigorous style of foraging activity. Therefore, behavioral strategies to avoid heat loss may be of more importance for the survival of this small mustelid than the capacity for high RMR.

The absolute value of the slope of the regression line through metabolic rates at temperatures below thermoneutrality is a measure of minimum conductance. The value calculated for marten in this study (0.0527 ml O_2 /g x hour x $^\circ$ C) was greater than the 0.0334 ml O_2 /g x hour x $^\circ$ C predicted for an animal of this body mass ($C = 1.05M^{-0.51}$, Bartholomew 1977), but closer to the 0.046 ml O_2 /g x hour x $^\circ$ C reported for marten by Worthen and Kilgore (1981). An explanation for the higher conductance by our marten may be their lower RMR due to behavioral differences in the experimental situation (Korhonen et al. 1983).

The measured $\underline{T}_{lc}$ in this study (16°C) approximates the predicted $\underline{T}_{lc}$ = 20 C ($\underline{T}_{lc} = \underline{T}_{b} - 4M^{0.23}$; Bartholomew 1977) for similar-sized mammals in spite of the lower RMR. This value, however, is considerably lower than the 29°C calculated by Worthen and Kilgore (1981).

The $\underline{T}_{lc}$ determined for our six winter-acclimated marten was 13°C below that reported by Worthen and Kilgore (1981), but higher than any ambient air temperature recorded during the study period (Figure 5). Air temperatures recorded at climate stations in the study area did not exceed 16 C between September 17, 1985 and May 2, 1986. Although the $\underline{T}_{lc}$ of marten in winter was lower than predicted by body size, marten are not as adapted to severe cold through the growth of highly insulative fur as are some cold climate mammals. Hart et al. (1965) found that the $\underline{T}_{lc}$ of winter-acclimated varying hares (Lepus americanus) from Ontario, Canada (mean weight = 1.5 kg) was -5°C, and Irving et al. (1955) reported a $\underline{T}_{lc}$ for winter-acclimated red foxes (Vulpes vulpes) of -13°C. In addition, Underwood (1971) found that winter-acclimated arctic foxes (Alopex lagopus), weighing only 4.1 kg, had $\underline{T}_{lc}$ s lower than -40°C, the limit of his environmental chamber. Clearly, the morpho-logical adaptations of marten to cold are inferior to those of some ecologically similar mammals; marten would pay high energetic costs to rest at $\underline{T}_{a}$ in winter. Therefore, the thermodynamics of resting and characteristics of resting sites are critical factors in the survival of this animal.

Three energetic options appear overriding in their importance during resting. First, marten can reduce their $\underline{T}_{b}$ to decrease the

thermal gradients across the body surface. Second, marten can select sites that are warm relative to $\underline{T}_a$ and that can be further warmed by the heat loss associated with $\underline{T}_b$ changes at the onset of resting. Lastly, they can increase thermogenic activities to accomodate high rates of heat loss that would occur at microenvironmental temperatures ($\underline{T}_{me}$ s) below thermoneutrality.

We found that marten thermoregulated at rest by the coordinated use of the first two tactics. Free-ranging marten depressed $\underline{T}_b$ by a mean of 2.9°C during resting episodes. Assuming a $\underline{Q}_{10}$ of 2.0, marten would achieve a 14.5% reduction in metabolic energy consumption below normothermic ($\underline{T}_b$ = 38°C) levels. $\underline{T}_b$ depression of this magnitude would produce a deep sleep, but not the torporous symptoms characteristic of more profound $\underline{T}_b$ depression (Hudson 1978). We estimated daily energy savings from $\underline{T}_b$ depression by assuming that marten rested for 12 hours daily, depressed $\underline{T}_b$ by a maximum of 2.9°C during each resting episode, and conformed to the $\underline{T}_b$ curves in Figures 2 and 3. Estimated daily savings of energy were 4.0%. Assuming $\underline{T}_b$ depression of 5.1°C, rate of energy use while resting would be reduced by 25.5%, and daily energy costs by about 6.4%.

Resting in protected sites and increasing their insulative properties by lining them with such things as prey fur (MacLean et al. 1974, Erlinge 1980) can provide an effective strategy for reducing heat loss (Lynch 1974). From related and concurrent studies, we found that marten were selective in their use of resting sites, prefering sites that were generally below the snow

surface and associated with coarse woody debris (Buskirk et al. submitted). These subnivean resting sites have T_{me} s of a nearly constant -2.5 to -1.0°C, which is generally warmer than T_a, but 15° C below the T_{lc} of marten, a circumstance experienced by other small mustelids (MacLean et al. 1979). Resting sites within stumps and logs, may, in addition, be warmed by the heat loss from resting marten. Thus, reduction of T_b during resting has two potentially important energetic consequences, to lower T_{lc} and to raise T_{me}.

The rise in T_b prior to leaving resting sites resembles patterns found in muskrats (MacArthur 1979) and red squirrels (Pauls 1979). These small mammals depress T_b while resting in protected sites, but rely upon agility and alertness to avoid predation outside the nest. Therefore, it is important to raise T_b to a level that allows alertness and coordinated movement before leaving the protection of the resting site. For these rodents and for marten, T_b recovery prior to the onset of activity may have important implications for predator avoidance.

Depth of T_b depression and duration of resting episodes were entrained to environmental cues. Resting T_b s were keyed to T_a, which marten were exposed to during the preceeding activity period. Changes in T_a had vanishingly small daily effects on the T_{me} of subnivean sites, so it seems unlikely that resting marten could respond to T_a in real time. Pauls (1979) found a similar correlation between T_b and T_a in red squirrels (Tamiasciurus hudsonicus) during winter. Marten also exhibited more profound depression of T_b during long resting episodes than during brief

ones. Presumably, the thermal inertia of marten bodies precluded profound $\underline{T}_b$ depression and recovery during brief resting episodes.

Marten exhibited keen behavioral sensitivity to weather conditions. The strong correlation of resting episode duration with the cooling power of the air during the preceeding activity period indicates that marten set the duration of resting episodes in response to environmental conditions while active, rather than to conditions that prevailed at the time of resting. This approach permited marten to recover from cold exposure for periods that were wind chill-dependent. Marten were active almost every day, even during the lowest temperatures and highest winds observed during the study period. However, when marten were exposed to high winds and low temperatures, they remained in their resting sites for longer than normal periods later the same day. Zielinski et al. (1983), studying marten in the Sierra Nevadas, concluded that marten timed their daily foraging activities to coincide with those of their nocturnal prey rather than to minimize heat loss. Although our data do not contradict theirs, we did find a marked effect of cold, windy weather on activity. We hypothesize that marten set the duration and timing of daily activities to optimize individual fitness rather than in response to a single environmental factor. We predict that marten will modulate the budget and timing of resting, foraging and other behaviors in a coordinated response to weather factors, patterns of prey activity and the activity patterns of potential predators and competitors of this forest carnivore.

CONCLUSIONS

This investigation showed that American marten occupy an environment with T_a s during winter far below a laboratory-measured T_{lc} of 16°C. Marten depressed T_b during daily resting episodes. Deepest depression of T_b during resting episodes averaged 2.9°C. The most profound depression of T_b observed during a single resting episode was 5.1°C. Resting was strongly entrained to environmental cues. Duration of resting episodes was correlated with the cooling power of the air during the immediately preceeding activity period. Mean daily energy savings from T_b modulation was estimated at 4.0%. Marten appear to thermoregulate at rest by the coordinated use of metabolic quiescence, occupation of protected microenvironments, and behavioral sensitivity to weather factors.

ACKNOWLEDGEMENTS

This project was made possible by funding from the National Geographic Society; the U.S.D.A. Forest Service, Rocky Mountain Forest and Range Experiment Station; and the Office of Research, University of Wyoming. We wish to thank the Wyoming Game and Fish Department for technical support, and the Forest Service for permission to conduct field work in the Medicine Bow National Forest. The University of the Wilderness allowed us to use their Snowy Range Laboratory. Louise R. Forrest provided invaluable assistance during the field studies.

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Figure 1. Location map for study area.

Figure 2. Mean body temperatures of four free-ranging marten in winter in relation to time of entrance into resting sites. Bars indicate $\pm$ 1 standard error. Sample sizes are number of data runs for each study animal.

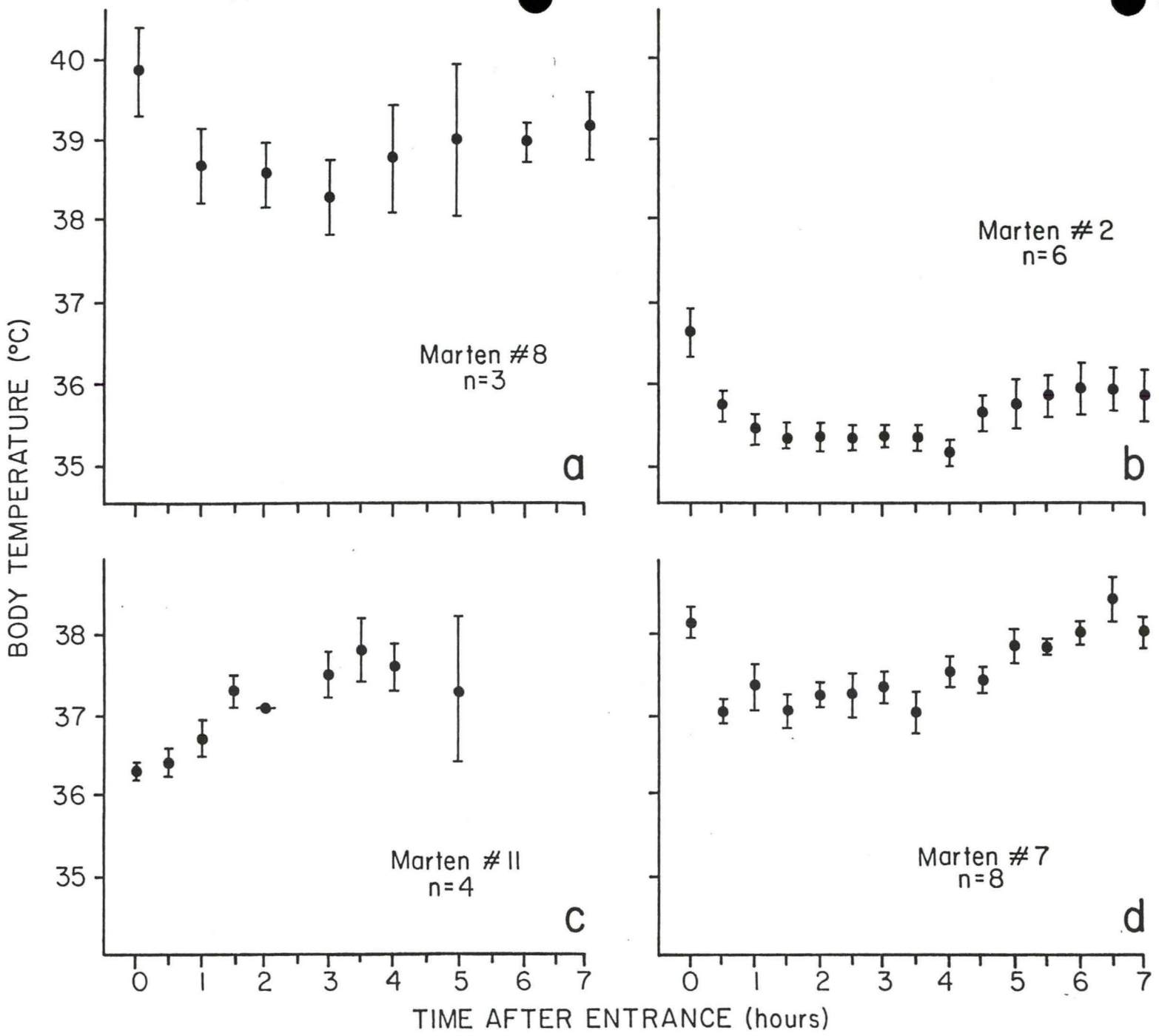

BODY TEMPERATURE (°C)
40
39
38
37
36
35
Marten #8
n=3
a
Marten #2
n=6
b
38
37
36
35
Marten #11
n=4
c
Marten #7
n=8
d
0
1
2
3
4
5
6
7
TIME AFTER ENTRANCE (hours)

Figure 3. Mean body temperatures of six free-ranging marten in winter in relation to time of departure from resting sites. Data are standardized to $\underline{T}_b$ at time of departure and pooled for all study animals. Bars indicate $\pm$ 1 standard error.

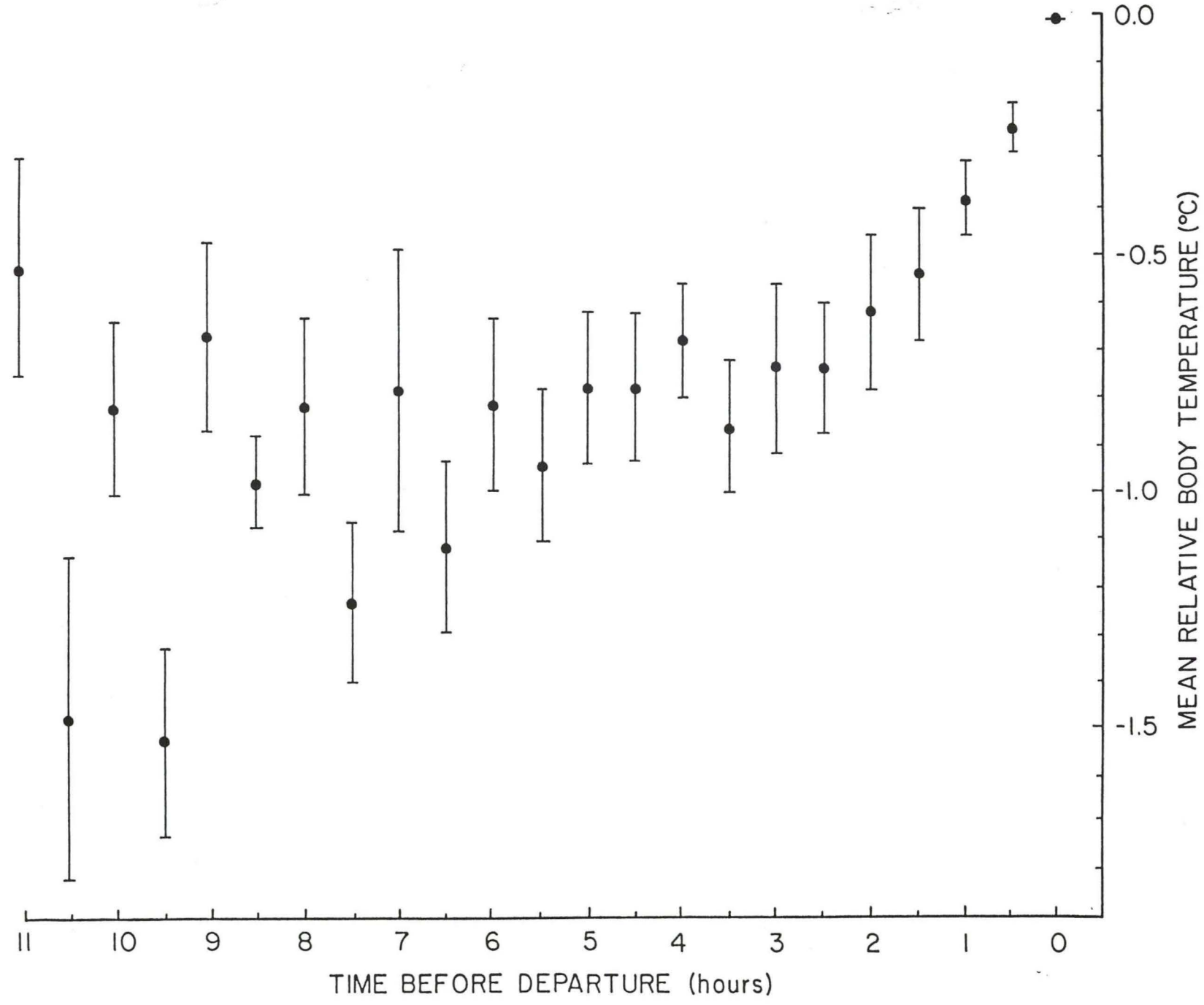

0.0
-0.5
-1.0
-1.5
MEAN RELATIVE BODY TEMPERATURE (°C)
11
10
9
8
7
6
5
4
3
2
1
0
TIME BEFORE DEPARTURE (hours)

Figure 4. Metabolic rate in relation to air temperature for 6 winter-acclimated American marten.

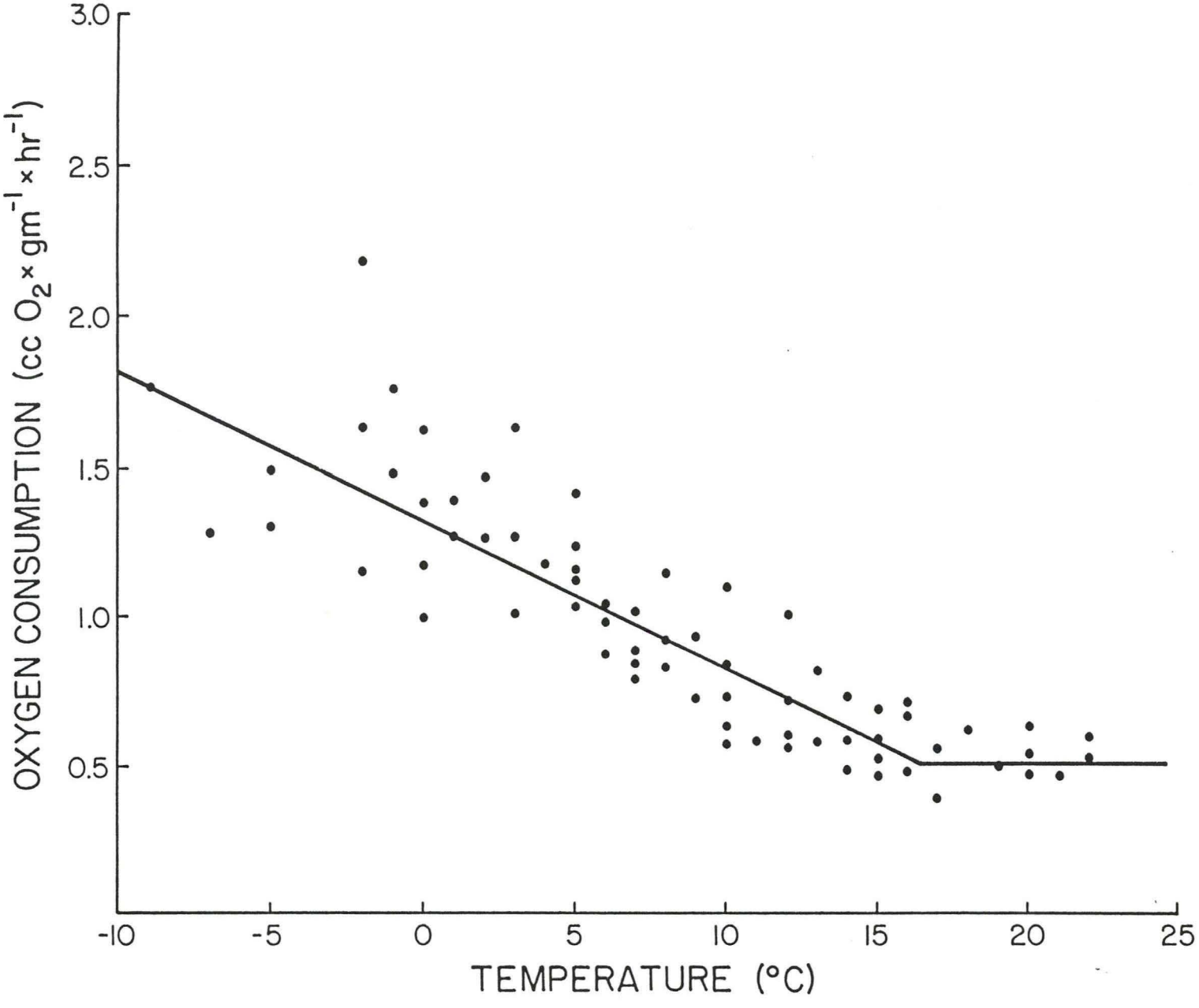
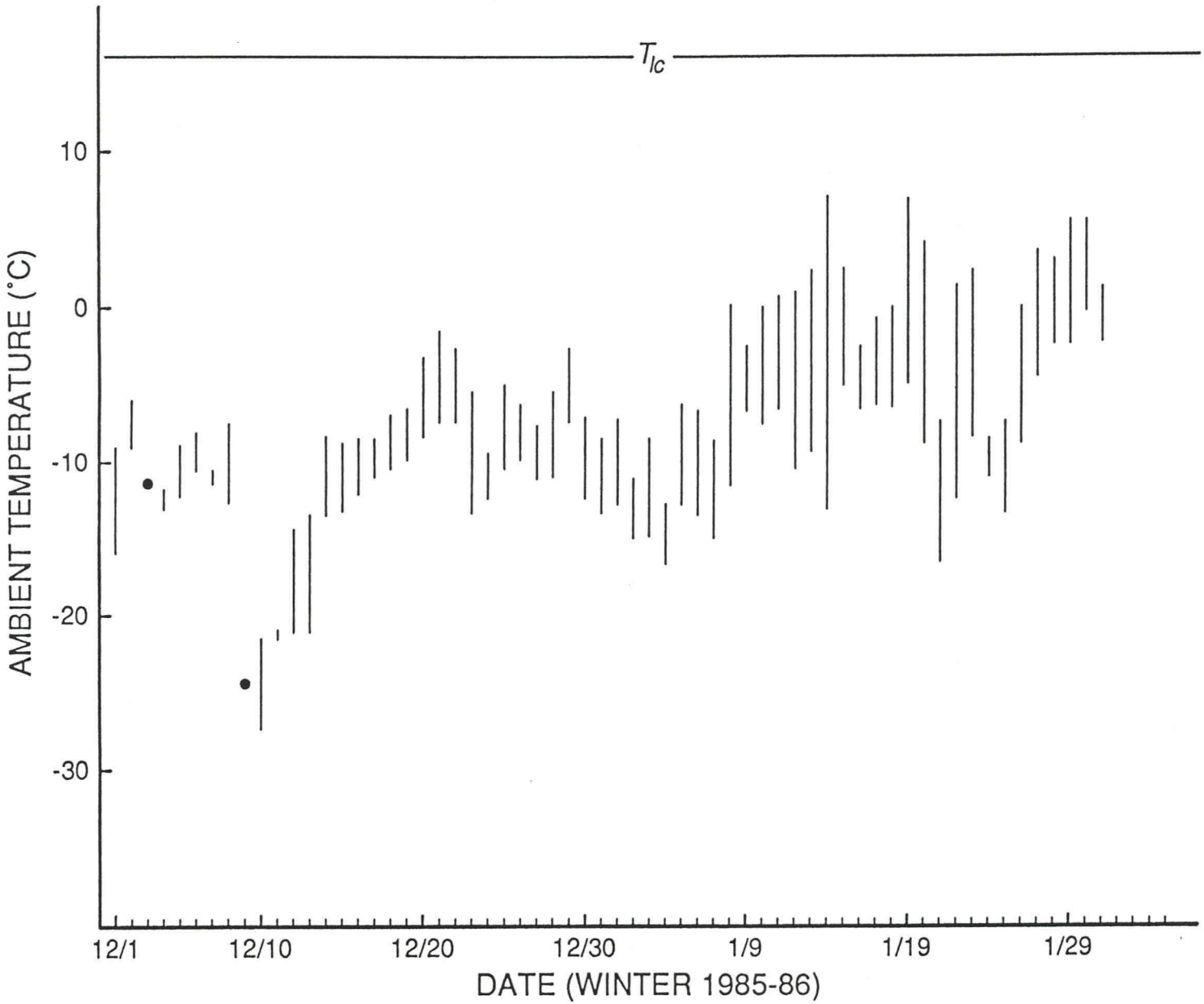

OXYGEN CONSUMPTION (cc O_2 × gm^{-1} × hr^{-1})
3.0
2.5
2.0
1.5
1.0
0.5
-10
-5
0
5
10
15
20
25
TEMPERATURE (°C)

Figure 5. Ambient temperatures at 3012 m in the study area for December 1985 and January 1986 in relation to the measured lower critical temperature of winter-acclimated marten.



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